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Factors determining the frequency and productivity of double brooding of Barn Owls

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Capsule: Early nesting Barn Owls (*Tyto alba*) and those that switched nest sites fledged most chicks overall because they could fit two more productive, nesting attempts into a breeding season.

Aims: To determine the frequency and productivity from double broods in Barn Owls, and for double brooders, what affects the probability of nest switching, and how it affects productivity.

Methods: We monitored the first egg date of each nesting attempt, whether it was in a "vole year", whether a breeding attempt was first or a second annual attempt, the number of chicks fledged from each attempt, and whether a pair switched nest sites, if breeding twice, from 602 Barn Owl breeding attempts in an area of lowland England from 1996-2007. General linear models were used to determine predictors of the probability that a pair had a second brood and the number of chicks fledged in each nesting attempt, and then for those owls that double brooded, which variables best predicted the probability of switching, and the number of chicks fledged from the second nest. Finally, we tested whether switching resulted in a shorter laying interval and higher annual productivity.

Results: Early nesting birds were more likely to double brood, although this was relaxed in vole years when later nesting birds also double brooded. Productivity (through increased numbers of chicks fledged or reduced chick loss) was higher the earlier a nest occurred, and there were more chicks fledged in good vole years and in second nesting attempts. Productivity, brood depletion, first clutch date and vole years did not determine whether a double brooding pair switched nesting sites. Productivity in the second nest did not change with a switch but productivity increased for early first nests and second nests with a shorter interval between the first and second nest. Switching however decreased nesting interval and nesting interval was also less if there were fewer fledglings from the first nest. Overall productivity was higher for pairs that switched.

Conclusions: Double brooding in Barn Owls increases seasonal productivity substantially and its occurrence depends critically on vole abundance or early nesting. Nest switching between broods may be a strategy for earlier laying of the second brood. Provision of alternative nest sites, close together in a Barn Owl's home range, may allow earlier re-nesting and so increase productivity.

Introduction

Repeated breeding in a season, even after a successful first nest, can be an important component of population dynamics for temperate bird species that have seasonal time constraints (Lack 1950, e.g. Kershner et al. 2004, Podolsky et al. 2007, Monroe et al. 2008, Mulvihill et al. 2009). Many factors favour the evolution or maintenance of this important life-history trait, such as food availability (Nagy & Holmes 2005a, Moore & Morris 2005), parental investment strategies (Szekely et al. 1999, Pope & Crawford 2001) length of the breeding season (Jamieson 2011, Jacobs et al. 2013) or conflict with other activities such as moult (Ogden & Stutchbury 1996) or migration (Ligi & Omland 2007). But in general, selection almost always acts to promote breeding as early as possible (Crick et al. 1997): time is then available to increase reproductive fitness by re-nesting after initial failure, or by multiple brooding, if resources level allow (Husby et al. 2009, Seward et al. 2014).

One potential further consideration for the occurrence of repeated breeding in a season may be availability of nests sites, because a second nest site may allow a second brood to be started earlier, even before the first has fledged, so allowing the second brood to start early enough to complete within seasonal time constraints (Batchelder et al. 2012). Cavity nesters, however, are often severely constrained in terms of nest site availability (Newton 1998) and this may well limit starting second broods sufficiently early enough to be successful. Understanding such factors that contribute to species breeding again, even after a successful first brood, may therefore be important in the understanding and conservation management of both expanding and declining populations (Nagy & Holmes 2004, Nagy & Holmes 2005b, Curtis et al. 2005).

The Barn Owl *Tyto alba* is a species that has long been known to double brood but this behaviour is not often studied (e.g. Beziers & Roulin 2016, Marti 1994) because it requires detailed repeated monitoring of breeding attempts and careful recording of clutch dates for both attempts. Its occurrence depends predominantly on food supply (reviewed in Beziers & Roulin 2016). Barn Owls breed earlier in the year, in greater numbers and are more productive in high ‘vole years’ (Pavluvcik et al. 2015). In ‘vole years’ in the United Kingdom, an abundant food supply of species such as the short-tailed field vole *Microtus agrestis* (which can represents in excess of 70% of the diet in the UK), promotes early clutch initiation and above average clutch size (Shawyer 1994). By laying early in the year, the

breeding season can be extended and fitter individuals, or those in more prey rich habitats, have the opportunity to lay a second clutch (Beziers & Roulin 2016) provided that an abundant food supply remains available from April to July (the normal breeding season). The breeding period from egg to fledging is at least three months and because they are asynchronous, a brood of 5-7 can be in the nest for nearly four months before the youngest has fledged. To breed successfully twice in one season therefore requires an ample food supply for a minimum of six months from April to September and depending on the time between attempts and the size of both broods, chicks can be fledging from the second attempt as late as October or early November. Barn Owls are particularly susceptible to inclement weather and in a temperate region such as the United Kingdom are subject to cold and rainy conditions which can directly affect/limit foraging success and ultimately brood productivity, particularly late in the breeding season (Marti 1994, Chausson et al. 2014, Toms 2014).

As well as food supply, double brooding in Barn Owls could also be constrained by nest site availability. By 2005, 70% of the UK population was breeding in nest boxes (Shawyer 2006) and lack of sufficient nest sites particularly those located close to good foraging habitat, has long been recognised as one of the main causes of population limitation (Debruijn 1994, Meyrom et al. 2009). Indeed, this may remain a significant factor affecting the number of double brooding events in the UK. Because early nesting is crucial to productivity in Barn Owls and broods are asynchronous, extending the fledging period, using a second site may allow the species to start a second brood earlier (Beziers & Roulin 2016). Here we examine data from a detailed long term study of breeding Barn Owls over several ‘vole cycles’, where a part of the study site has been saturated with nest boxes (placed at approximately 1 km intervals) – so constraints of lacking the details of the timing of all seasonal nesting events, food availability and the availability of nest sites for second broods have been removed. This then allows us to measure and examine what determines the frequency and success of double broods and how this might lead to increased productivity during a period of rapid population recovery for the species. First, we confirm the confounding effects of food availability and nest timing on Barn Owl productivity: we test whether:

1. the probability that a pair has a second brood depends on the number of chicks fledged and lost from the first nest, laying date and whether it was a vole year.

2. the number of chicks fledged (a) or number of chicks (b) lost in each nesting attempt depends on nest type (1st of 1 only nest; 1st nest of a double brood and 2nd of a double brood), and whether this is affected by laying date or vole years.

Second, we then examine, for those owls that double brood, what affects the probability of switching and how nest switching affects productivity. We test whether:

1. switching to a new nest site depends on the number of chicks fledged and lost from the first nest, laying date and whether it was a vole year.

2. the number of chicks fledged (a) or number of chicks lost (b) in the second nest depends on whether a pair switches, laying date, the interval between 1st and 2nd nesting attempts and whether it was a vole year.

3. switching results in a shorter nesting interval, controlling for the number of chicks fledged in the first nest, laying date and whether it was a vole year.

4. the total number of chicks fledged is higher for owls that switch, controlling for the laying interval between nests, laying date and whether it was a vole year.

Methods

The study was carried out in a contiguous region of approximately 2,500 square kilometres in three South Midland counties of England (1°15" to 0°0" W - 51°59" to 52°46"N) comprising three distinct geographical zones. a) The Peterborough area (150sq/km): a flat low lying homogenous 'fen' landscape with intensive arable farming separated by a network of ditches and dykes. b) Northamptonshire county (2300 sq/km): an area of gently rolling mixed farmland typical of lowland England in the mid and upper catchments of the River Nene. c) The Upper Ouse Valley (10 sq/km): an area of north Buckinghamshire, primarily permanent pasture on the river floodplain and separated from the River Nene Valley by a low watershed. Altitude varies from sea level in the east to a maximum of 222m in the Northamptonshire uplands in the west. Only a small proportion of land (less than 0.001%) lies above 180m, the altitude above which Barn Owls do not normally breed regularly in Great Britain (Shawyer 1994). During the study period from 1995-2007 mean annual rainfall was

640mm and annual mean temperature 8-10°C based on data from University of Northampton climatological records.

Following the UK's conservation plan for this bird (Shawyer 1987) and later its published strategy (Brazil & Shawyer 1992), the number of nest sites was increased throughout the three areas during the project period as more artificial nest boxes were installed, natural sites identified and habitat quality improved. Artificial nest site types varied between the three areas described (Table 1*).* Sites in Northamptonshire and the Ouse Valley were located primarily along the main river corridors at approximately 1km spacing with boxes on poles arranged in pairs. Pole boxes were generally paired with another pole box but occasionally with tree, or barn boxes at distances varying from 25-500m. In the Peterborough area, there was an even distribution of mainly barn boxes approximately 1-2km apart. Barn boxes in Northamptonshire were randomly located along main river corridors complementing the more evenly distributed pole and tree boxes and were sometimes associated with known natural tree sites.

All Barn Owl nest boxes and known natural sites were monitored at least once during the breeding season. Where necessary, sites with known breeding attempts, and any sites nearby, received second or multiple visits to complete data and check for second attempts. First checks took place from March to June to determine where pairs were breeding. Clutch size, pulli numbers, weight, and a "food score" was recorded. Food was scored on a 4-point scale where, food 0 = empty and hungry and 3 = well and recently fed – this was used to confirm vole years: a food score of 2 or 3 for all pulli in a brood was an indication that ample food was available. Length of emerging 7th primaries were recorded in order to age chicks and establish lay dates. The pulli were aged by measuring length of emerged seventh primary based on a chart of feather growth rates (Shawyer 1994). The age of the eldest was used to calculate the laying date based on an assumed incubation period of 31 days. There was a small error estimating laying date if first laid eggs fail to hatch or chicks were found dead in the nest. The latter was more likely in poor breeding seasons when brood depletion was greater and may have occurred prior to first visits. It was assumed that fledging occurred 60 days after hatching. All pulli aged over 21 days were ringed. Sometimes more than one visit was required to complete ringing and confirm brood

size. Multiple visits enabled brood depletion to be calculated and the number fledging to be accurately established.

Whenever possible but avoiding disturbance, adults were captured, weighed, sexed, and moult and brood patch status recorded following the nest recording methods developed by Shawyer (Toms et al. 2001). All captured adult birds were either ringed or previous ring details recorded. Any adult primary and secondary moult feathers deposited in or close to a breeding site were collected, measured, and used to help verify age and sex of adults based on individual feather length and the known moult sequence (Shawyer 1998).

Second checks took place from August to October at all sites where breeding had occurred earlier in the year. Other known sites in the vicinity or within home ranges of original breeding sites were also inspected at this stage in order to check for possible second breeding attempts at switched sites. In Northamptonshire and Buckinghamshire there was potential for breeding to take place at other unknown natural sites within a home range. In the fen landscape around Peterborough there were very few natural alternative sites or unoccupied nest boxes. Consequently, it was less likely that second broods were not recorded. Where breeding was confirmed the monitoring process was the same as for first checks earlier in the year.

As the project progressed we became confident that any pairs that began to lay first eggs after 30th April were unlikely to breed twice. Having established this, in the last two years of the project, the monitoring effort for second broods was generally confined to pairs beginning first attempts on or before 30th April. During random checks of adjacent sites, no egg laying dates later than 30th April for first attempts by double breeding pairs were recorded.

The individual identity of adult birds was confirmed where possible through ringing and recapture with due diligence and the need to avoid disturbance at critical times in the breeding cycle. The project utilized frequent but sensitive monitoring and recording, together with local knowledge of habitats, foraging patterns, and timing of breeding to obtain sufficient data to establish a minimum level of double breeding attempts in the population. Both male and female adults were confirmed at approximately 5% of breeding attempts but very few for both first and second attempts. Although Barn

Owls generally pair for life (see Dreiss & Roulin 2014), both sexes can change partners within a breeding season (Beziers & Roulin 2016). Therefore, some of the recorded attempts may have involved either male or female from a second breeding pair being different from the first pair. It was assumed this affected relatively few pairs because only four possible such events were recorded from 122 double brooding pairs monitored. A concurrent Swiss study involving an intensive ringing program found that 46% of females and 4% of males were birds that changed partners for the second attempt (Roulin 2002).

Statistical analysis

During the twelve-year study period from 1996-2007 a total of 602 breeding attempts by 509 pairs were monitored of which 111 pairs had two broods in any one season. A separate sub-set of data was used to record results for all pairs where both first and second attempts were monitored and whether second attempts were in the original natal site i.e. non-switchers (N = 61) or switchers (N = 52) in an alternative location. Sample sizes for individual analyses are detailed in Tables 2-7; these vary because of missing data, for example, where all chicks were found dead at the nest before age of eldest could be established.

Hypotheses as detailed in the last part of the introduction were tested with Generalised Linear Mixed Models with binomial logistic error structure or Linear Mixed Models with a normal error structure depending on whether we were testing what affected probability of double brooding or switching, or whether we were testing what affected number of chicks fledged, lost, the interval between the date that the clutch was initiated in the first and second nest or overall productivity respectively. All models included county within year as random effects to control for the uneven sampling between counties and years. A relatively small proportion of the same pairs contributed more than one year's data. We have ignored this level of pseudo-replication because we cannot fully account for it because both individuals in each pair were not always ringed and/or captured. Predictors included in models, where relevant were: number of chicks lost, number of chicks fledged, Julian date of start of first clutch, vole year (whether a year was a vole year or not), nest type (1st of 1 only nest; 1st nest of a double brood and 2nd of a double brood), nest interval (the interval between the date that the clutch was initiated in the first and second nest), and switch (whether a pair switched nesting sites for their second nest or

not). Interactions between predictors and vole year were tested for all models where relevant because it might be expected that any relationships constrained by food availability would be relaxed in vole years: none were found to be significant in any model and were not considered further. Models were run in R version 3.1.3 (R Development Core Team 2013) using the library nlme.

Results

Second broods represented 18.4% of all breeding attempts (N = 602). With the exception of 2003 there were double broods in all years although 82% (91) occurred in the vole years of 2002, 2004, 2005 and 2007 when prey availability was high (Table 2). Double brooded pairs represented 37.7% of the breeding population and produced 41% of the owlets fledged from both attempts.

The probability that a pair had a second brood depended significantly on laying date (earlier higher probability, -0.08 $\pm$ 0.01, z = -6.2, P < 0.001) and whether it was a vole year (higher probability in a vole year, 1.5 $\pm$ 0.5, z = 2.8, P = 0.005) but not on the number of chicks fledged (0.1 $\pm$ 0.1, z = 0.9, P = 0.35) or lost from the first nest (0.1 $\pm$ 0.2, z = 0.6, P = 0.51; overall N = 456): Figure 1. The number of chicks fledged in each nesting attempt depended significantly on nest type (no difference between 1st of 1 only nest and 1st nest of a double brood, but 0.95 more chicks for the 2nd nest of a double brood; Figure 2) and lay date (more chicks for early nests; Figure 2), with a marginally significant increase of 0.6 chicks in vole years (Figure 2; Table 3a). The number of chicks lost in each nesting attempt only depended significantly on lay date (slightly more chicks lost in later nests) but not on nest type or whether it was a vole year (Table 3b).

For pairs that had a second nesting attempt, the probability that they switched nest sites did not depend on the number of chicks fledged (0.1 $\pm$ 0.2, z = 0.8, P = 0.44) or lost from the first nest (0.6 $\pm$ 0.4, z = 1.4, P = 0.17), laying date (0.01 $\pm$ 0.02, z = 0.7, P = 0.47) and whether it was a vole year (1.4 $\pm$ 1.1, z = 1.3, P = 0.22; overall N = 111). The number of chicks fledged in the second nesting attempt depended significantly on lay date (more chicks for early nests; Figure 3) and the interval between the date that the clutch was initiated in the first and second nest (fewer chicks as nest interval increased; Figure 3), but did not depend on whether a pair switched nest sites for the second nest or whether it was a vole year or not (Table 4a). The number of chicks lost in the second nesting attempt was not

dependent on whether a pair switched nest sites, lay date, whether it was a vole year or the interval between the date that the clutch was initiated in the first and second nest (Table 4b). The interval between the date that the clutch was initiated in the first and second nest was significantly less by 17 days for pairs that switched nest site (Figure 4) and increased significantly as the number of chicks fledged from the first nest increased (Figure 4) and lay date of the first nest occurred earlier, but there was no effect of vole year (Table 5). The total number of chicks fledged by double brooders in a season was significantly greater by 1.7 chicks if a pair switched nest sites (Figure 5) and decreased significantly with later first nesting attempts, but there was no effect of whether it was a vole year or not or the interval between the date that the clutch was initiated in the first and second nest (Table 6).

Discussion

We found that early nesting birds were more likely to double brood, although this was relaxed in vole years when later nesting birds could also double brood. Productivity (through increased numbers of chicks fledged or reduced chick loss) was higher the earlier a nest occurred, and there were more chicks fledged in good vole years and in second nesting attempts. Productivity, brood depletion, first clutch date and vole years did not determine whether a double brooding pair switched. Productivity (although solely through increased numbers of chicks) in the second nest did not change with a switch but productivity increased for early first nests and for second nests that got started after a shorter interval between the first and second nest. Switching however decreased nesting interval and nesting interval was also less if there were fewer fledglings from the first nest. Finally, we found that overall productivity was higher for pairs that switched. Overall, early nesting owls and those that switched nest sites fledged most chicks because they could fit two more productive nesting attempts into a breeding season.

Our results confirm the importance of early nesting and food availability to annual productivity in Barn Owls (Marti 1994, Martinez & Lopez 1999, Beziers & Roulin 2016). To breed twice a female needed to begin the first clutch by 30th April. Double breeders began first attempts significantly earlier than single breeders by a mean of 26 days but not in vole years; however in a Spanish study there was little inter annual variation in prey abundance and the mean laying date for first clutches did not differ for pairs laying one or several clutches (Martinez & Lopez 1999). The 'decision' on whether to lay a second

clutch occurs early during the breeding cycle and probably two to three weeks after the laying of the first egg of the first clutch. At that point with abundant food, the female will either initiate or delay moult with the prospect of commencing a second breeding cycle (Roulin 2002). It has been suggested (Bunn et al. 1982) that the second breeding cycle begins about seven weeks after first hatching. In the Scottish population (Taylor 1994) the interval between start of first and second clutches averaged 98 days, and this was 99 days in a Spanish study (Martinez & Lopez 1999), compared with a mean of 109 days for this study. The shorter period in Scotland may be due to the more northerly latitude, where longer daylight and greater food abundance in peak vole years promote earlier laying of second clutches (Taylor 1994), but in the Spanish study there was little inter annual variation in prey abundance which suggests that the more favourable climate rather than latitude was the main influence (Martinez & Lopez 1999). In a Swiss study the interval between clutches varied from 83-91 days for deserting females at switched sites and 91-104 days for those non-deserters that did not switch (Roulin 2002).

Approximately half of second attempts were in switched sites and were begun about two weeks earlier than at sites of non-switchers. Site switching rates in Beziers & Roulin's study (2016) were slightly lower than in our study, but first egg dates in switched sites were also about 2 weeks earlier than in non-switched sites. The probability of switching in our study did not depend on the productivity of the first attempt or the laying date; this was also the case for Beziers & Roulin's (2016) study. More likely it was due to the opportunity afforded by the close proximity of other potential nest sites whether natural or artificial. We have no data on mate switching between broods but Beziers & Roulin's (2016) study showed that those females that switched sites and that did not divorce their male from the first brood, bred relatively close to their original sites, suggesting that availability of a second nest site nearby may also influence speed of re-nesting through pairs remaining together.

Our results also show the importance of nest site switching to annual productivity in Barn Owls, but mainly in the context of facilitating earlier nesting: nest site switching per se probably does not lead to greater productivity when controlling for the effects of the earlier nesting that it allows (see also Beziers & Roulin 2016). Furthermore, although first broods of double breeders were not significantly more productive in terms of fledglings produced or chicks lost compared to single breeders in our and

285 Beziers & Roulin's (2016) study, this is only after controlling for laying date: double breeders in both
286 studies started nesting earlier. Second broods of double breeders were, however, more productive
287 compared to single breeders, controlling for laying date and food supply, suggesting that it is only
288 better quality Barn Owl pairs or those in better habitats that can breed twice. Double brooding also
289 clearly leads to much higher overall productivity: if we assume an average interval between clutches
290 then a double brooding Barn Owl pair will produce about 4 more chicks from both attempts (double the
291 annual productivity of a single breeder in a non-vole year).

292 We conclude that double brooding pairs could be a major contributor to population growth in Barn
293 Owls. Productivity was much higher, and importantly, unpublished data suggests that there was
294 minimal difference first winter survival for chicks fledging from first attempts (8.8%, N = 1299
295 recaptures and recoveries) compared with second attempts (6.1%, N = 294 recaptures and
296 recoveries). First attempts needed to have begun no later than 30th April to create the opportunity to
297 breed twice and although early breeding was a pre-requisite for a second attempt it did not guarantee
298 it. But by switching sites for second attempts Barn Owls could probably be more successful because
299 they could re-nest earlier. Therefore, the availability of alternative nest sites within the home range
300 may be important to facilitate early laying of second clutches and site switching between broods. The
301 availability of nest sites was particularly high in our study: future studies should provide 1 or 2 nest
302 boxes in close proximity per Barn Owl territory to experimentally test whether increased availability
303 causes higher productivity by allowing more Barn Owls to be able to start a second brood early
304 enough. In our study, distances between nest boxes used for first and second broods varied
305 considerably (see Table 1) but were of the order of a few hundred meters.

306 Barn owls are unique among raptors and are known to double brood in most regions of the world
307 provided there is an ample supply of food. They have evolved to respond to cyclical changes in food
308 supply by maximizing reproduction in times of plenty and reducing reproductive effort in times of prey
309 scarcity. In the UK they are at the northern most latitude of world range and are subject to 'Atlantic'
310 weather and associated extreme climatic events which impact on food availability and successful
311 foraging (Taylor 1994). Therefore, in this context, it is probable that double brooding, although
312 important as a breeding strategy may be less successful in Great Britain than in other regions with

more stable environments. Nevertheless, it provides a mechanism for rapid population growth when food and nest sites are not limiting. The effects of double breeding on fecundity in subsequent years, understanding the role of each sex and the biological process that stimulate double brooding, survival rates, and the optimum siting of alternative nest sites are opportunities for further research to better understand this. In the meantime, however, it seems that provision of at least two nest sites in close proximity per pair may well facilitate increased number of, and more successful double brooding attempts and so population growth in Barn Owls.

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References

Batchelder, N., Batchelder, G., Livezey, D. A. & Marks, J. S. 2012. Simultaneous Multiple Nests of Calliope Hummingbird and Rufous Hummingbird. *Wilson Journal of Ornithology,* **124:** 640-643.

Beziers, P. & Roulin, A. 2016. Double brooding and offspring desertion in the barn owl Tyto alba. *Journal of Avian Biology,* **47:** 235-244.

Brazil, M. A. & Shawyer, C. R. 1992. The Barn Owl, The Farmer's Friend Needs a Helping Hand. London: The Hawk & Owl Trust.

Bunn, D. S., Warburton, A. B. & Wilson, R. D. S. (1982) *The Barn Owl,* London: A & C Black Publishers Ltd.

Chausson, A., Henry, I., Almasi, B. & Roulin, A. 2014. Barn Owl (Tyto alba) breeding biology in relation to breeding season climate. *Journal of Ornithology,* **155:** 273-281.

Crick, H. Q. P., Dudley, C., Glue, D. E. & Thomson, D. L. 1997. UK birds are laying eggs earlier. *Nature,* **388:** 526.

Curtis, O., Malan, G., Jenkins, A. & Myburgh, N. 2005. Multiple-brooding in birds of prey: South African Black Sparrowhawks Accipiter melanoleucus extend the boundaries. *Ibis,* **147:** 11-16.

Debruijn, O. 1994. Population ecology and conservation of the Barn Owl *Tyto-alba* in farmland habitats in Liemers and Achterhoek (The Netherlands). *Ardea,* **82:** 1-109.

Dreiss, A. N. & Roulin, A. 2014. Divorce in the barn owl: securing a compatible or better mate entails the cost of re-pairing with a less ornamented female mate. *Journal of Evolutionary Biology,* **27:** 1114-1124.

Husby, A., Kruuk, L. E. B. & Visser, M. E. 2009. Decline in the frequency and benefits of multiple brooding in great tits as a consequence of a changing environment. *Proceedings of the Royal Society B-Biological Sciences,* **276:** 1845-1854.

Jacobs, A. C., Reader, L. L. & Fair, J. M. 2013. What determines the rates of double brooding in the Western Bluebird? *Condor,* **115:** 386-393.

354 Jamieson, S. E. 2011. Pacific Dunlin Calidris alpina pacifica show a high propensity for second clutch
355 production. *Journal of Ornithology,* **152:** 1013-1021.

356 Kershner, E. L., Walk, J. W. & Warner, R. E. 2004. Breeding-season decisions, renesting, and annual
357 fecundity of female eastern meadowlarks (Sturnella magna) in Southeastern Illinois. *Auk,* **121:**
358 796-805.

359 Lack, D. 1950. The breeding seasons of European birds. *Ibis,* **92:** 288-316.

360 Ligi, S. & Omland, K. 2007. Contrasting breeding strategies of two sympatric orioles: first
361 documentation of double brooding by Orchard Orioles. *Journal of Field Ornithology,* **78:** 298-
362 302.

363 Marti, C. D. 1994. Barn owl reproduction - patterns and variation near the limit of the species
364 distribution. *Condor,* **96:** 468-484.

365 Martinez, J. A. & Lopez, G. 1999. Breeding ecology of the Barn Owl (*Tyto alba*) in Valencia (SE
366 Spain). *Journal fur Ornithologie,* **140:** 93-100.

367 Meyrom, K., Motro, Y., Leshem, Y., Aviel, S., Izhaki, I., Argyle, F. & Charter, M. 2009. Nest-box use by
368 the Barn Owl Tyto alba in a biological pest control program in the Beit She'an valley, Israel.
369 *Ardea,* **97:** 463-467.

370 Monroe, A. P., Hallinger, K. K., Brasso, R. L. & Cristol, D. A. 2008. Occurrence and implications of
371 double brooding in a southern population of Tree Swallows. *Condor,* **110:** 382-386.

372 Moore, D. J. & Morris, R. D. 2005. The production of second clutches in the common tern: Proximate
373 effects of timing and food supply. *Waterbirds,* **28:** 458-467.

374 Mulvihill, R. S., Latta, S. C. & Newell, F. L. 2009. Temporal constraints on the incidence of double
375 brooding in the Louisiana Waterthrush. *Condor,* **111:** 341-348.

376 Nagy, L. R. & Holmes, R. T. 2004. Factors influencing fecundity in migratory songbirds: is nest
377 predation the most important? *Journal of Avian Biology,* **35:** 487-491.

378 Nagy, L. R. & Holmes, R. T. 2005a. Food limits annual fecundity of a migratory songbird: An
379 experimental study. *Ecology,* **86:** 675-681.

380 Nagy, L. R. & Holmes, R. T. 2005b. To double-brood or not? Individual variation in the reproductive
381 effort in Black-Throated Blue Warblers (Dendroica caerulescens). *Auk,* **122:** 902-914.

382 Newton, I. (1998) *Population limitation in birds,* London: Academic Press.

383 Ogden, L. J. E. & Stutchbury, B. J. M. 1996. Constraints on double brooding in a Neotropical migrant,
384 the Hooded Warbler. *Condor,* **98:** 736-744.

385 Pavluvcik, P., Poprach, K., Machar, I., Losik, J., Gouveia, A. & Tkadlec, E. 2015. Barn Owl Productivity
386 Response to Variability of Vole Populations. *Plos One,* **10**.

387 Podolsky, A. L., Simons, T. R. & Collazo, J. A. 2007. Modeling population growth of the ovenbird
388 (Seiurus aurocapilla) in the southern appalachians. *Auk,* **124:** 1359-1372.

389 Pope, M. D. & Crawford, J. A. 2001. Male incubation and biparental care in Mountain Quail. *Condor,*
390 **103:** 865-870.

391 Roulin, A. 2002. Offspring desertion by double-brooded female Barn owls (Tyto alba). *Auk,* **119:** 515-
392 519.

393 Seward, A. M., Beale, C. M., Gilbert, L., Jones, T. H. & Thomas, R. J. 2014. The Impact of Increased
394 Food Availability on Reproduction in a Long-Distance Migratory Songbird: Implications for
395 Environmental Change? *Plos One,* **9**.

396 Shawyer, C. R. 1987. The Barn Owl in the British Isles: Its Past, Present and Future. London: The
397 Hawk Trust.

398 Shawyer, C. R. (1994) *The Barn Owl,* London: Hamlyn.

399 Shawyer, C. R. (1998) *The Barn Owl,* Chelmsford: Arlequin Press.

400 Shawyer, C. R. 2006. What makes owls tick? *Adopt a box news,* **28:** 4-5.

401 Szekely, T., Cuthill, I. C. & Kis, J. 1999. Brood desertion in Kentish plover: sex differences in remating
402 opportunities. *Behavioral Ecology,* **10:** 185-190.

403 Taylor, I. R. (1994) *Barn Owls: Predator–Prey Relationships and Conservation,* Cambridge:
404 Cambridge University Press.

405 Toms, M. (2014) *Owls,* London: Collins New Naturalist.

406 Toms, M. P., Crick, H. Q. P. & Shawyer, C. R. 2001. The status of breeding Barn Owls Tyto alba in the
407 United Kingdom 1995-1997. *Bird Study,* **48:** 23-37.

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409

410 Table 1: Number of monitored nesting sites by type during the study.

411

	Peterborough	Northamptonshire	Ouse Bucks	Total	Percentage
Barn Boxes	72	71	1	144	43%
Tree Boxes	11	44	15	70	21%
Pole Boxes	9	69	17	95	28%
Natural Sites	3	22	1	26	8%
Total	95	206	34	335	100%

412

413

414 Table 2: Sample size of 1st broods only (N = 380) and double broods (N = 111) split by year (vole
415 years in bold), with mean (and SE) of first egg dates for the first brood for single broods and the first
416 brood for double broods and the mean distance between nests for double broods.

417

	Single broods				1st of 2 broods				Distance between	
Year	N	1st egg date			N	1st egg date			1st and 2nd brood (m)	
		Mean		SE		Mean		SE	Mean	SE
1996	4	May	5	9	4	April	9	5	350	202
1997	24	April	18	2	4	April	13	4	363	166
1998	20	May	7	5	2	April	13	1	0	0
1999	24	May	2	8	5	April	3	3	520	174
2000	26	May	9	7	1	March	24		0	
2001	33	May	8	3	1	April	14		100	
2002	21	April	14	5	20	April	6	3	246	109
2003	24	May	31	6	0					
2004	32	May	3	4	18	April	12	3	178	139
2005	51	April	22	4	13	April	2	2	572	245
2006	58	May	7	3	3	April	9	5	133	133
2007	62	April	23	3	40	April	6	2	155	50

418

Table 3: What determines number of chicks fledged (a) or the number of chicks lost per nesting attempt (b). Results from a LMM of number of chicks ~ nest type (1st of 1 only nest; 1st nest of a double brood and 2nd of a double brood) + Julian date of start of first clutch + whether a year was a vole year or not, with random effects of county within year. Interactions with vole year were not significant in either model. N = 553. Significant P values in bold. Intercept is 1st of 1 attempt; non-vole year.

a. Number of fledglings	Est.	SE	t	P value
Intercept	4.08	0.44	9.4	<0.001
1st of 2 attempts	0.01	0.18	0.04	0.97
2nd of 2 attempts	0.95	0.32	3.0	**0.003**
Julian date	-0.01	0.003	-4.4	**<0.001**
Vole year	0.59	0.28	2.1	0.056
b. Number of chicks lost				
Intercept	-0.08	0.12	-0.7	0.50
1st of 2 attempts	0.04	0.05	0.7	0.49
2nd of 2 attempts	0.04	0.09	0.4	0.70
Julian date	0.003	0.001	3.3	**0.002**
Vole year	-0.05	0.06	-0.8	0.43

Table 4: Is the number of chicks fledged (a) or lost (b) in the second nest higher with a switch? Results from a LMM of number of chicks ~ Julian date of start of first clutch + whether a year was a vole year or not + nest interval (the interval between the date that the clutch was initiated in the first and second nest), with random effects of county within year. There were no significant interactions between vole year*switch in either model. N = 97. Significant P values in bold. Intercept is no nest site switching between broods and non-vole year.

a. No. chicks fledged 2nd nest	Est.	SE	t	P value
Intercept	18.3	2.7	6.8	<0.001
Switch	0.12	0.39	0.29	0.77
Julian date	0.09	0.02	-5.9	**<0.001**
Vole year	0.01	0.84	0.01	0.99
Nest interval	-0.06	0.01	-4.1	**<0.001**
b. Number of chicks lost				
Intercept	0.24	0.51	0.5	0.65
Switch	0.02	0.07	0.3	0.81
Julian date	0.001	0.003	0.4	0.72
Vole year	0.02	0.21	0.1	0.94
Nest interval	-0.002	0.003	-0.7	0.50

Table 5: Does switching result in a shorter laying interval between 1st and 2nd nests? Results from a LMM of nest interval (the interval between the date that the clutch was initiated in the first and second nest) ~ whether a pair switched nesting sites for their second nest or not + number of chicks fledged from the 1st nest + Julian date of start of first clutch + whether a year was a vole year or not, with random effects of county within year. N = 97. Significant P values in bold. Intercept is no nest site switching between broods and non-vole year.

	Est.	SE	t	P value
Intercept	134.6	11.1	12.1	<0.001
Switch	16.6	2.3	7.2	**<0.001**
No. chicks fledged	3.0	0.8	3.7	**<0.001**
Julian date	-0.23	0.1	-2.30	0.03
Vole year	-5.4	4.8	-1.1	0.29

Table 6: Does the total number of fledglings increase with a switch? Results from a LMM of the total number of chicks fledged from both nests in a season ~ whether a pair switched nesting sites for their second nest or not + Julian date of start of first clutch + whether a year was a vole year or not + nest interval (the interval between the date that the clutch was initiated in the first and second nest), with random effects of county within year. Interactions with vole year were not significant. N = 97. Significant P values in bold. Intercept is no nest site switching between broods and non-vole year.

	Est.	SE	t	P value
Intercept	14.9	3.8	4.0	<0.001
Switch	1.7	0.57	3.0	**0.004**
Julian date	-0.1	0.02	-4.4	**<0.001**
Vole year	0.92	1.3	0.70	0.50
Nest interval	-0.01	0.02	-0.5	0.60

455 Figure legends
456

457 Figure 1: The probability of double brooding depended on the date that the first clutch was initiated
458 and whether it was a vole year. Predicted lines are from the model in Table 2 for the median number
459 of fledglings. Black solid line mean predicted value in non-vole years (dashed black lines ± 1 standard
460 error); grey solid line mean predicted value in vole years (dashed grey lines ± 1 standard error).

461

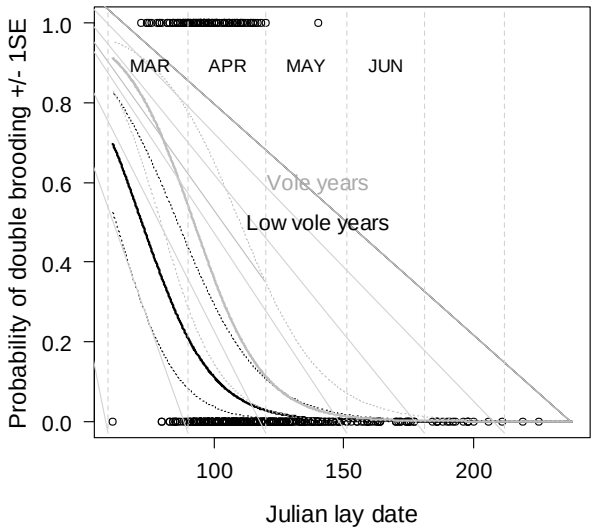
462 Figure 2: Top panel; the variation in number of chicks fledged with nest type (1/1 = 1st of 1 only nesting
463 attempt; 1/2 = 1st nest of 2 attempts and 2/2 = 2nd of 2 attempts) and whether it was a vole year.
464 Predicted values are plotted from the model in Table 3a for a nest starting on the median first egg date
465 for first nest. Bottom panel; the variation in number of chicks fledged with the date that the first clutch
466 was initiated. Predicted values are plotted from the model in Table 3a for the 1st nest of 1 only attempt
467 and a non-vole year.

468 Figure 3: Top panel; the number of chicks fledged in a second nest with the date that the first clutch
469 was initiated. Predicted values are plotted from the model in Table 4a for median nesting interval.
470 Bottom panel; the number of chicks fledged in a second nest with the interval between the date that
471 the clutch was initiated in the first and second nest. Predicted values are plotted from the model in
472 Table 4b for median date that the first clutch was initiated.

473 Figure 4: Effect of switching nest site (same nest site circles, black lines; change in nest site triangles,
474 grey lines) on the interval between the date that the clutch was initiated in the first and second nest
475 with the number of fledglings produced from the 1st nest. Predicted values are plotted from the model
476 in Table 5 for vole year and for median date that the first clutch was initiated (± 1 standard error as
477 dashed lines).

478 Figure 5: The total number of chicks fledged from both nests with whether a pair used the same nest
479 site or shifted. Predicted values are plotted from the model in Table 6 for median date that the first
480 clutch was initiated and a median interval between the date that the clutch was initiated in the first and
481 second nest.

482 Figure 1



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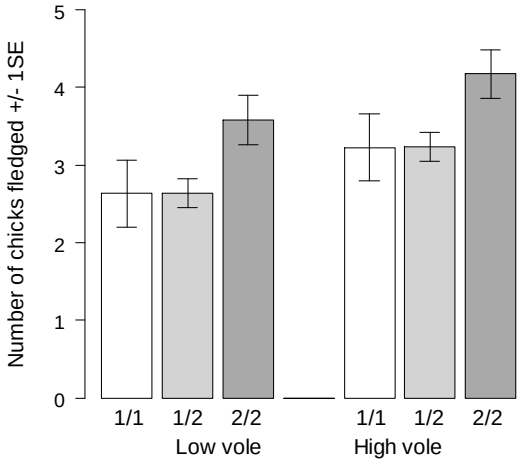

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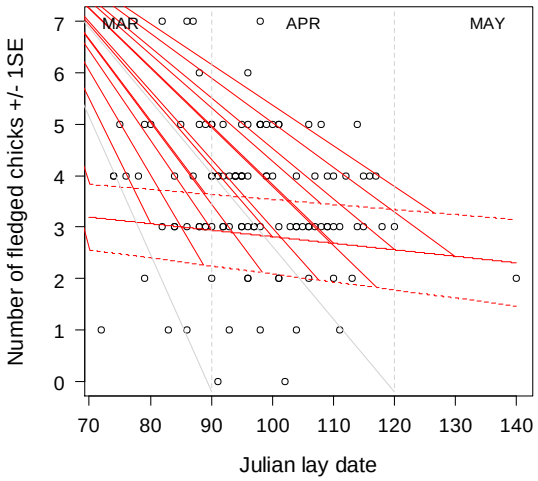

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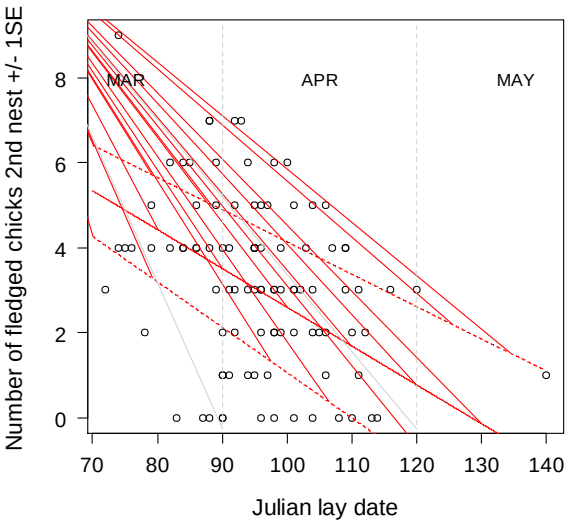

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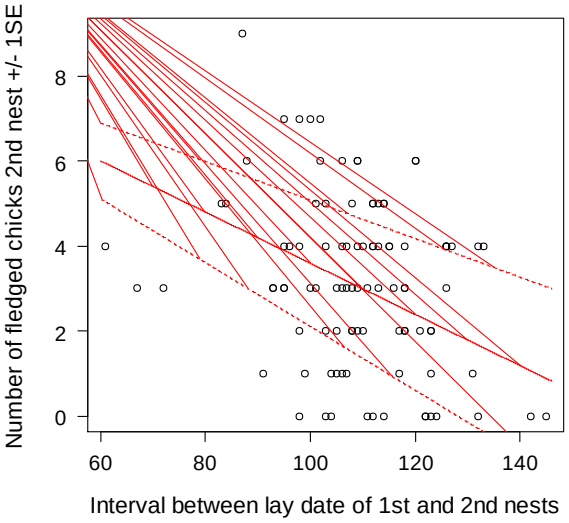

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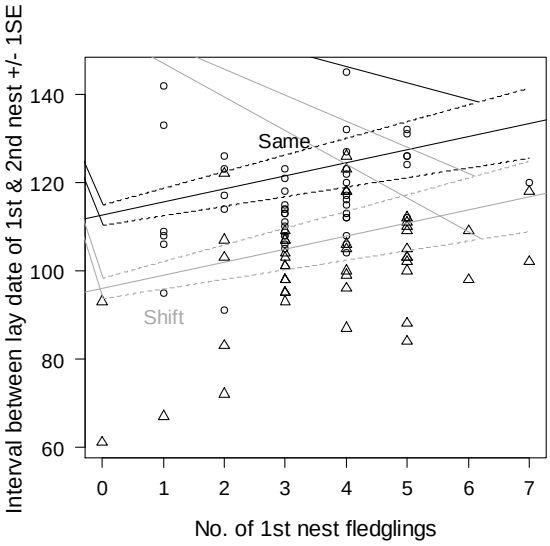
493 Figure 4



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496 Figure 5:
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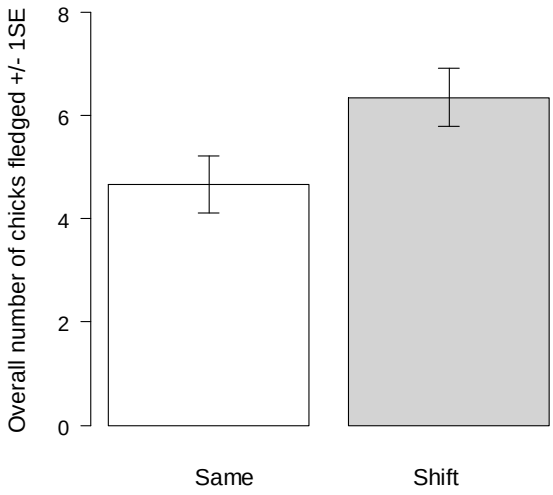

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